DINOFLAGELLATE CYSTS FROM THE GLACIAL/POSTGLACIAL TRANSITION IN THE NORTHEAST ATLANTIC OCEAN

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ABSTRACT. High-resolution dinoflagellate cyst analysis of two DSDP holes and two British Gcological Survey cores, from the drift ridges on the south-western and south-eastern flanks of the Rockall Plateau and the continental slope off western Scotland respectively, has yielded detailed cyst spectra across the glacial/postglacial transition. These spectra illustrate clearly the substantial climatic and palaeoceanographic changes that have accompanied deglaciation over the last 13 Ka and the enigmatic short-term return to the cooler conditions of the Younger Dryas. The dinoflagellate cyst assemblages have undergone changes both in species composition and in the numbers of cysts per gram recovered but show consistent and repeatable evidence of fluctuations within the dinoflagellate cyst floras. Comparisons are made with earlier studies and with recently published work from the Norwegian Sea, which together indicate substantial detail within the Holocene climatic record, and are interpreted as representing considerable oceanographic variability throughout the last 10 Ka.

OVER recent years, there has been increased interest in the nature and timing of the glacial/postglacial transition in the north-eastern Atlantic Ocean. Attention to this phenomenon has continued to grow since the advent of the CLIMAP studies (Cline and Hays 1976) and the increased availability of DSDP and ODP material, and of the many cores taken by other research organizations including the British Geological Survey (BGS). This interest in the last deglaciation partly stems from an increased ability to model the dynamic changes involved in the shift from a fully glacial world, at about 18 Ka, to the 'interglacial' conditions of today and partly in its implications for the future.

The last deglaciation was not a gradual event but rather non-linear in character (Duplessy *et al.* 1986; Bard *et al.* 1987). In particular, the importance of a short-lived and unexpected reversal in the warming trend, the Younger Dryas, was realized. The dynamics of this reversal and the rate of change of the underlying causes have proved to be of great concern, and are particularly relevant to predictive modelling of oceanographic change as the greenhouse effect vies with the orbital-forcing mechanisms in determining the possible future climate of the Earth.

This Younger Dryas reversal, in an otherwise warming trend, fits into the currently understood deglaciation history as follows (after Ruddiman 1987). The period from full glacial conditions (18 Ka) to about 13 Ka included winter sea-ice to about 50 °N in the North Atlantic Ocean but perhaps with sufficient annual variation to have large ice-free areas during some winters; sea level at the time of maximum glaciation was about 121 m below present sea-level (Fairbanks 1989). During the period 13 to 11 Ka the polar front retreated to the north-west allowing warmer, more saline, water from the subtropical gyre into the eastern and central North Atlantic. This was then followed from 11 to 10 Ka (the Younger Dryas) by an advancement of the polar front to a location close to its position during full glacial times. After 10 Ka the polar front again retreated to the north-west into the south-eastern Labrador Sea, where it remains today.

It has been suggested from foraminiferal evidence that there was seasonal ice cover in the Norwegian Sea during the Younger Dryas (Sejrup *et al.* 1984). This was before the later influx of the North Atlantic Current (NAC), as the polar front retreated to its present position, at about

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10 Ka. The Holocene warming continued from 10 Ka to a maximum interglacial configuration at about 6 Ka (Ruddiman and McIntyre 1981). Spectral analysis of Late Pleistocene/Holocene sediments has revealed a periodicity of 380 yrs and 2.6 Ka akin to the known ¹⁴C fluctuations in the atmosphere associated with solar activity (Pisias *et al.* 1973; Keigwin and Jones 1989). Historically, this cyclicity may have been recognized earlier with the establishment of the Blytt–Sernander vegetational zones of continental Scandinavia (Sernander 1908). These vegetational changes also appear to have a cyclicity of about 2.5 Ka, like that recorded by Denton and Karlén (1973) in a study of the Holocene glacial extensions in the Yukon and Alaska.

Furthermore, the Younger Dryas is also remarkable for the rate of change that marks its inception and end. The advance of the polar front at the beginning of the period appears to have occurred over less than 100 years (Ruddiman 1987) and its retreat in as little as 20 years (Dansgaard *et al.* 1989). The assessment of these rates of change is dependent on good chronostratigraphical control. Recent dating of a core by Bard *et al.* (1987), taken in the Rockall area close to the present study area, placed the Younger Dryas between 11 500 and 10700 YBP. The Younger Dryas is, therefore, commonly regarded as being about 1000 years in duration. This is too short for a simple response to orbital-forcing (Ruddiman 1987), but certainly not too short a time for the North Atlantic Ocean to undergo major changes in its circulation regime. The origin and timing of this 'catastrophe' is not understood, but may involve a small disturbance unbalancing a somewhat chaotic system (Berger 1990).

Many of the explanations currently espoused involve the shutting down of the production of North Atlantic Deep Water (NADW) by, for instance, the lowering of the North Atlantic surface temperature and reducing the flux of nutrient-depleted northern source water into the deep Atlantic (Boyle and Keigwin 1987). One way of lowering the surface temperature is by introducing cold, fresh meltwater from the waning Laurentide ice sheet. This would also have the effect of reducing surface salinities and density, and so lessening the efficacy of the formation of NADW, thus slowing the North Atlantic 'conveyor' (Broecker et al. 1988, 1989). Recently it has been suggested that the ice sheet disintegration occurred in two steps, as evidenced by rapid rises in sea-level at 12 and 9.5 Ka (Fairbanks 1989) and by the accompanying major decreases in ¹⁸O and increased deep water formation and ventilation during the Younger Dryas (Jansen and Veum 1990). Although the Younger Dryas is regarded as a brief return to glacial conditions, Jansen and Veum (1990) believed that the formation of NADW in the Younger Dryas is more like the situation today than that at full glacial times. Finally, the recent work of Kudrass et al. (1991) and Mathewes et al. (1993) belies the notion of the Younger Dryas being a predominantly north-west European phenomenon. This argues against a parochial North Atlantic cause and may point to global lowering of atmospheric CO₃ (Kudrass *et al.* 1991).

Undoubtedly the controversy will continue, and remain inextricably linked to the production and strength of NADW. Recent insights suggest both a rapid shutdown of NADW circulation during the Younger Dryas, based upon geochemical data derived from planktonic foraminifera (Lehman and Keigwin 1992), and that deep ventilation was as vigorous then as it is today, based upon benthic foraminiferal isotope information (Veum *et al.* 1992). The timing and nature of the last deglaciation is a complex phenomenon, but vitally important to the testing of our predictive skills and perhaps finally to our future well-being.

The ability to model and interpret this last deglaciation requires not only an understanding of the physical changes, but also the consequences of these changes on the biological component. The effects of deglaciation have long been demonstrated by both floral and faunal populations, but it is only recently that dinoflagellate cysts have been utilized to provide information for both climatic and oceanographic reconstruction (Harland 1988; De Vernal *et al.* 1992). This has proved possible only in the light of increasing knowledge of the ecology of dinoflagellates and their cysts (Dale 1983; Harland 1988). Recently, quantitative attempts have been made to use dinoflagellate cyst assemblages as proxies for palaeotemperature estimates (Edwards *et al.* 1991, Mudie 1992).

Dinoflagellates are part of the plankton, but their cysts act as benthos (Dale 1983) providing a unique opportunity to access information from both these important regimes within the ocean.

However, careful consideration of this information is required before any interpretations are attempted (Evitt 1985) since the cyst assemblages do not exactly mirror the motile dinoflagellate populations. A commentary on dinoflagellates, their cysts and their usefulness in elucidating Quaternary climatic change may be found in Harland (1988, 1992*a*).

It is against this background that the dinoflagellate cyst record of the Glacial/Postglacial transition is being studied to assess its contribution to the understanding of the last deglaciation of the North Atlantic Ocean. Turon (1978, 1980, 1981) has demonstrated that indeed there were significant changes in the dinoflagellate cyst assemblages during this time and that they may relate to movements of the surface water masses. Recent investigations (Stoker *et al.* 1989) have indicated the potential of dinoflagellate cyst analysis in elucidating the effects of bottom water currents, whereas most recently Baumann and Matthiessen (1992) have used dinoflagellate cyst assemblages and coccolith data to investigate surface water mass conditions through the Holocene of the Norwegian Sea. This contribution aims to further the use of dinoflagellate cysts in assisting the understanding of the last deglaciation and the postglacial history of the northeastern Atlantic Ocean.

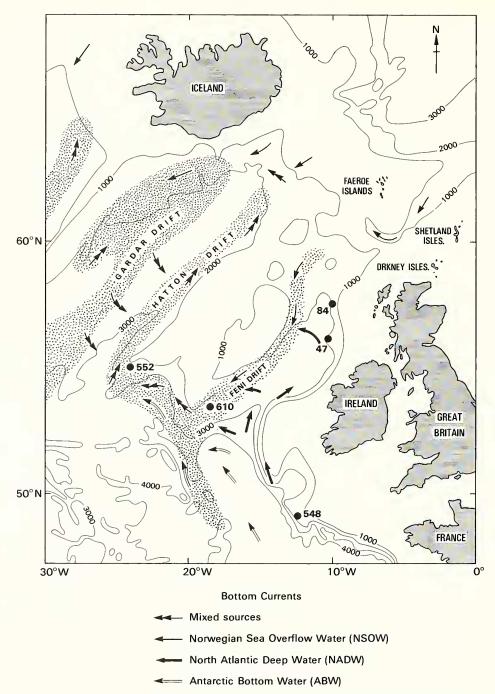
MATERIALS AND METHODS

Four cored sequences that are known to span the Glacial/Postglacial transition were chosen for study. Their localities and water depths are indicated in Table 1 and Text-figure 1. Sample numbers and depth/core data arc given in Appendix 1; all samples, preparations and data sheets are held in the palynological collections of the Biostratigraphy and Sedimentology Group, BGS, Keyworth.

TABLE 1. Core Localities.

Core	Location	Water depth (m)	Samples
DSDP 552A	Lat: 56° 02·56′ N Long: 23° 13·88′ W	2301	10
DSDP 610A	Lat: 53° 13·30′ N Long: 18° 53·21′ W	2417	10
BGS Vibrocore 57/-10/84	Lat: 57° 37·33′ N Long: 09° 49·19′ W	1346	21
BGS Gravity Core 57/-10/47	Lat: 56° 23·22′ N Long: 09° 57·98′ W	1787	21

Standard preparation techniques were used throughout but the numbers of cysts per gram of sediment were always calculated using the method described in Harland (1989). The majority of the subsequent text-figures, using these data, are drawn to the same scale to allow close comparison; however, the scale for Text-figure 4 has been adjusted to allow for formatting. Some measure of chronostratigraphical control is provided by the oxygen isotope stratigraphy where available. The two sets of data from the DSDP Holes are aliquots from samples used to establish the stable isotope stratigraphy and, therefore, offer a first-order correlation between the biostratigraphy and the stable isotope data. The oxygen isotope data for DSDP Hole 552A is based upon that quoted for the benthic foraminifer *Cibicidoides wuellerstorfi* (Schwager) whereas that from DSDP Hole 610A is based upon the planktic foraminifer *Neogloboquadrina pachyderma* (Ehrenberg). All chronological control for the Younger Dryas is based upon the work of Bard *et al.* (1987). In addition a taxonomic listing of the taxa encountered is provided in Appendix 2 with reference to recent illustrations. Discussions on the taxonomy of Quaternary dinoflagellate cysts are to be found in Harland (1982, 1983).



TEXT-FIG. 1. Location map for DSDP Sites 552 and 610 together with BGS Sites 56/-10/47 and 57/-10/84. Contourite drift deposits are stippled and the various bottom water currents are shown.

RESULTS

Each of the four cores will be discussed in turn before more general interpretations and conclusions are reached and comparisons made. Unfortunately, high-resolution dinoflagellate cyst records are rare for this area (De Vernal *et al.* 1992), highlighting the relative paucity of dinoflagellate cyst analyses in investigating Late Pleistocene and Holocene sequences.

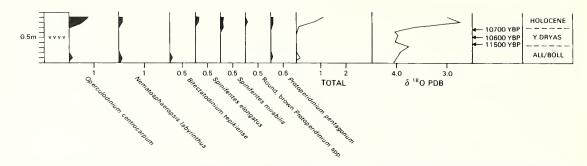
DSDP Hole 552A

Originally drilled as a part of DSDP Leg 81 on the south-western margin of the Rockall Plateau, this core proved a succession of sediments on the Hatton Drift (Roberts et al. 1984). It was one of the first DSDP holes to be drilled using the Hydraulic Piston Corer (HPC) and it provided a detailed stable isotope record indicating the initiation of glacial conditions at about 2.37 Ma in the North Atlantic, some 700 Ka before the Pliocene/Pleistocene boundary (Shackleton and Hall 1984). Also it provided evidence to suggest that, between 0.9 and 0.7 Ma, climatic cycles responding to the orbital obliquity rhythm (41 Ka) changed to ones responding to the eccentricity rhythm (100 Ka) (see Ruddiman and Wright 1987). The oxygen isotope signal from Hole 552A for the time span of interest, i.e. the youngest 1 m, is reproduced in Text-figure 2 after Shackleton and Hall (1984). The record appears to show a reasonable Termination IA, a poorer Termination IB and the Younger Dryas Interstadial; this allows for some chronostratigraphical control and the deduction of a maximum sedimentation rate of 300 mm per Ka during the Younger Dryas and about 70 mm per Ka for the Holocene. As discussed later, however, it is more than likely that the younger part of the Holocene is missing. Morton (1984) reported the presence of volcanic ash within Core 1 between samples at 0.38 m and 0.68 m with an extrapolated peak at 0.50 m; he tentatively correlated it with North Atlantic ash level I reported by Ruddiman and Glover (1975), dated at 9400 YBP, but now regarded as 10600 YBP (see Kvamme et al. 1989); this is also included on Text-figure 2.

The dinoflagellate cyst record of the Quaternary of Hole 552A was first discussed by Harland (1984) and subsequently by Harland (1989, 1992*b*) but detail of the last deglaciation was never described. Originally termed 'event 3' (Harland 1984) from Core 1, Section 1, it marked the incoming of rich and diverse dinoflagellate cyst assemblages and a changeover of dominance from *Bitectatodinium tepikiense* Wilson to *Operculodinium centrocarpum* (Deflandre and Cookson) Wall. This was noted as marking the onset of the present ameliorative climate. More detail of the dinoflagellate cyst assemblages of isotope stage 1 was given in Harland (1989) and interpreted in terms of the biological oceanography. However, until now no discussion of the deglaciation history has been given.

It is clear from Text-figure 2 and the data documented in Table 2 that the earlier part of the record, assumed to be Late Glacial in age and certainly > 10700 YBP, is characterized by a single productive sample at 0.9 m. This sample contains a dinoflagellate cyst assemblage characterized by low numbers of cysts per gram of sediment (< 50) and the species *Bitectatodinium tepikiense*, Nematosphaeropsis labyrinthns (Ostenfeld) Reid, Operculodinium centrocarpum and Protoperidinium pentagonum (Gran) Balech. This assemblage, although poor in numbers and diversity, contains elements suggestive of north-temperate climates, i.e. N. labyrinthus and P. pentagonum, and is possibly interpretable as assignable to the Allerød/Bölling Stade (see later). Between 0.4 and 0.1 m depth there is a second group of samples that yield dinoflagellate cyst assemblages. These assemblages give dinoflagellate cyst recovery figures of up to 1100 cysts per gram of sediment and are dominated by O. centrocarpum, accompanied by N. labyrinthus, P. pentagonum, Spiniferites elongatus Reid, and S. mirabilis (Rossignol) Sarjeant together with minor amounts of round, brown Protoperidinium cysts. The curve of the cyst numbers clearly shows a rising trend closely corresponding to the upward shift to progressively oxygen lighter water as the global ice volume decreased. As with the sample at 0.9 m, these assemblages are also interpreted as being northtemperate in nature and indicating environments similar to today. All three of these uppermost samples can, therefore, be assigned to the Holocene (see later).

DSDP HOLE 552 A



TEXT-FIG. 2. Dinoflagellate cyst spectrum for DSDP Hole 552A. X axis in thousands of cysts per gram. *P.* spp (RB) indet. indicates the counts of indeterminate round, brown *Protoperidinium* cysts.

Depth (m)	0.10	0.18	0.30	0.39	0.51	0.62	0.71	0.89	1.00
Gonyaulacaceae									
B. tepikiense								56	
N. labyrinthus	78	47						11	
O. centrocarpum	721	442						67	
S. elongatus	78	79							
S. mirabilis	117	63	34						
Peridiniaceae									
P. conicoides		16							
P. pentagonum	38	47	17					11	
<i>P</i> . spp. (RB)		47							
н	1033	741	51					145	

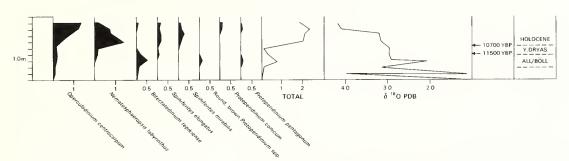
TABLE 2. DSDP Hole 552A—dinoflagellate cysts per gram.

DSDP Hole 610A

This hole was drilled as part of DSDP Leg 94 on the western side of the Rockall Trough at the crest of the Feni Ridge. It was drilled using the HPC and provided detail of the Neogene and Quaternary history of the ridge. Recently acquired and unpublished stable isotope data from Professor Eystein Jansen are included in Text-figure 3 with his permission. Unfortunately, there is obvious transportation and disturbance of the sediment at the top of the Hole giving glacial values (Jensen *in litt.*). Consequently, it appears that although Termination IA might occur at the base of the sequence studied, both Termination IB and the subsequent record are too disturbed to be recognized. Also, there are no detailed accounts of the sedimentology of the core so it is not possible to state if volcanic ashes are present. It has thus proved difficult to place the sequence in a time framework. However, the total dinoflagellate cyst recovery is good and appears not to have been affected by any disturbance; the reason for this is unknown. If the same chronostratigraphical assumptions are made, a maximum sedimentation rate of 150 mm per Ka for the Younger Dryas and about 80 mm per Ka for the Holocene follows. However, as with the record of 552A, it is likely that much of the later Holocene is missing.

Given that these assumptions are correct, the four main chronostratigraphical divisions, as illustrated in Text-figure 3, are characterized by different dinoflagellate cyst assemblages. All the dinoflagellate cyst data are given in Table 3. The assemblages are as follows; the latest glacial yields poor numbers of individuals but contains some *B. tepikiense* and *O. centrocarpum*; the

DSDP HOLE 610 A



TEXT-FIG. 3. Dinoflagellate cyst spectrum for DSDP Hole 610A. Legend as for Text-figure 2.

Depth (m)	0.12	0.30	0.40	0.60	0.75	0.90	1.06	1.20	1.35	1.48
Gonyaulacaceae										
B. tepikiense	17	_	_		_	111	471	78	12	24
I. aculeatum	_			_			13			
I. paradoxum		21				_				
N. labyrinthus	182	717	748	1385	111	100				
O. centrocarpum	1358	1209	888	399	78	122	178	22	38	_
S. elongatus	133	62	187	141		22				
S. mirabilis	50	164	257	47						
S. ramosus	_	—	_		_	11				
S. spp indet.	33	62				_	13		_	
Peridiniaceae										
P. pentagonum	33	21								
P. spp (RB)	_				_		38	_		
n	1806	2256	2080	1972	189	366	715	100	50	24

TABLE 3. DSDP Hole 610A—dinoflagellate cysts per gram.

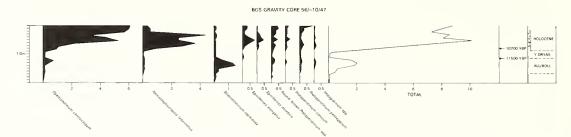
Allerod/Bölling has sharply increased numbers of cysts to c. 650 cysts per gram, consisting mainly of *B. tepikiense* with small numbers of *O. centrocarpum*, round, brown *Protoperidinium* cysts and *Impagidinium* species, together with the first appearance of *N. labyrinthus* and *S. elongatus*; the Younger Dryas has low numbers of cysts but includes *B. tepikiense*, *N. labyrinthus*, *O. centrocarpum* and *S. elongatus*; and finally the Holocene with cyst numbers in excess of 2200 cysts per gram and characterized by high numbers of *N. labyrinthus* and *O. centrocarpum* with *Impagidinium* spp., *P. pentagonum*, and *Spiniferites* cysts. *Nematosphaeropsis labyrinthus* exhibits a distinct peak abundance at 0.6 m at about the interpreted level of Termination IB.

Unfortunately the chronostratigraphy for DSDP Hole 610A has proved somewhat elusive, although the dinoflagellate cyst record appears to be particularly clear and more complete than that of Hole 552A.

BGS Gravity Core 56/-10/47

This gravity core was taken as part of the BGS survey of the British continental shelf and in particular to the production of the 1:250000 Quaternary Geology edition of the Peach Sheet (James 1991). Unfortunately no stable isotope or detailed sedimentology has been attempted on this core to date, despite its obvious interest. It is anticipated that some tephrachronological results may be available in future. However, for the moment the detailed dinoflagellate cyst analyses must stand

alone. The chronostratigraphy outlined in Text-figure 4 is, therefore, wholly interpretational based partly upon comparisons with the two DSDP Holes, discussed earlier, where there is some limited chronostratigraphy. A maximum interpreted sedimentation rate of 260 mm per Ka may have operated during the Younger Dryas, but the rate was more likely to have been about 50 mm per Ka for the Holocene. It is particularly clear that the record obtained from the dinoflagellate cysts is complete and well demonstrated within this gravity core. The dinoflagellate cyst spectrum is illustrated in Text-figure 4 and the data are given in Table 4.



TEXT-FIG. 4. Dinoflagellate cyst spectrum for BGS Gravity Core 56/–10/47. Legend as for Text-fig. 2. P. spp.
(P) indet. and P. spp. (RB) indet. refer to the indeterminate peridinioid and round, brown Protoperidinium species respectively. 1, Pre-Boreal; 2, Boreal; 3, Atlantic; 4, Sub-Boreal; and 5, Sub-Atlantic.

The Late Glacial part of the sequence is characterized by poor recovery of cysts (< 200 cysts per gram of sediment) but contains *B. tepikiense* and round, brown *Protoperidinium* cysts. The Allerod/Bölling Interstade, in contrast, demonstrates a marked increase in cyst recovery (> 500 to > 2000 cysts/gram) with high numbers of *B. tepikiense* and lesser numbers of round, brown *Protoperidinium* cysts, together with *Impagidinium* spp., *P. conicum* and *P. pentagonum*. *Operculodinium centrocarpum* is also notably present, coming to a peak of recovery slightly later than that of *B. tepikiense*; this undoubtedly has some oceanographic significance (see later). The Younger Dryas demonstrates a return to low recovery (< 200 cysts per gram) but is characterized by roughly equal amounts of *O. centrocarpum* and *B. tepikiense* together with round, brown *Protoperidinium* cysts. Finally the Holocene part of the interpreted sequence is characterized by markedly high cyst recovery (> 1000 to 10000 cysts per gram) with particularly high numbers of *O. centrocarpum* and *N. labyrinthus*. In addition *Spiniferites* species such as *S. elongatus* and *S. mirabilis* also show marked increases as do *Protoperidinium conicum*, *P. pentagonum* and round, brown *Protoperidinium* cysts.

This sequence is probably the most complete and full dinoflagellate cyst record for this part of the northeastern Atlantic and potentially offers a key to the interpretation of the palaeoceanography through the last deglaciation. A full discussion is given later.

BGS Vibrocore 57/-10/84

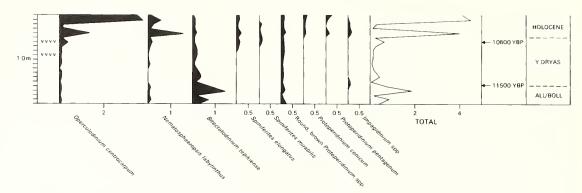
The second BGS core was also taken as part of the BGS survey of the United Kingdom continental shelf and, in particular, to the production of the 1:250000 Quaternary Geology St Kilda Sheet (Evans 1992). Although no stable isotope work is available, the core was analysed in detail for ash shards (Selby 1989) and, over the interval under discussion, two ash layers were discovered. The first downhole was at 0:60 m and the second at 0:90 m; these ashes may be correlated with the Vedde Ash at 10600 YBP and an earlier fall not previously recognized (Selby 1989). Assuming that the chronostratigraphy is approximately correct, the sequence is interpreted as in Text-figure 5. This implies a maximum sedimentation rate of about 1 m/Ka during the Younger Dryas and about 60 mm per Ka for the Holocene. It seems likely that parts of the Holocene are missing (see later).

The dinoflagellate cyst record for 57/-10/84 is illustrated in Text-figure 5 and documented in

Depth (m)	0.01	0-10	0.20	0-30	0.40	0.50	09-0	0.70	0.80	06-0	1.00	1·10	1.20	1.30	1.40	1·50	1-60	1.70	1.80	1.90	2.00
Gonyaulacaceae																					
B. tepikiense	117	113	4444	145	135	28	57	82	82	52	63	61	580	1237	1483	296	297	38	87	54	9
I. aculeatum				29	İ]		1	I	I				
I. paradoxum		28																	{		I
I. patulum							1							10			-]
I. sphaericum	29					28	I		27			18	32	70	32	I		4			
I. spp. indet.	-			29	81		113	110								1	Ι	I			
N. labyrinthus	379	507	548	4335	2453	2472	3683	2740	869	44		18	32	42	16	35				-	
O. centrocarpum	6034	6028	5673	3064	4366	5225	2266	1150	951	96	27	6	660	364	64	105	96	~	5		ļ
S. elongatus	291	310	143	87	431	815	482	137	82	I		6		I	16						
S. lazus						140	227	110	27						16					1	
S. membranaceus]						85					I			32						
S. mirabilis	29	28		145	270	421	28	82	82												
S. spp. indet.			29	116	27	112	283	301	109	6			32	10			16				
Peridiniaceae																					
A?. minutum						I					6										
P. conicoides						56]														
P. conicum	204	113	143	87	54	281		1	54					31		18					
P. pentagonum	166	254	315	116	81	56	142	247	136	18			32	31	32	35	24				1
P. subinerme			57			56		110			1			10							
P. sp. (P) indet.	117	85	86	58				55	109					42		105	112	4			
P. sp. (RB) indet.	525	479	315	347	162	421	113	356	217	105	36	18	258	218	112	87	32	4	52		1
Polykrikaceae P_schwart-ii		28		ł	54				1]]					I					
		2																			
11	8716	7973	7309	8558	8114 1	10111	7479	5480	2745	324	135	133	1626	2065	1803	681	577	58	114	54	9
																		1			

TABLE 4. BGS Gravity Core 56/-10/47-dinoflagellate cysts per gram.

BGS VIBROCORE 57/---10/84



TEXT-FIG. 5. Dinoflagellate cyst spectrum for BGS Vibrocore 57/-10/84. Legend as for Text-figure 2.

detail in Table 5. Pre Allerod/Bölling sediments appear to have not been penetrated but the interstade is characterized by high cyst recovery (> 500 to 1600 cysts per gram of sediment) and the dominance of *B. tepikiense*, although *O. centrocarpun*, *N. labyrinthus*, and round, brown *Protoperidinium* cysts together with *Inpagidinium* spp. are also present. In contrast, the Younger Dryas has low cyst recovery (< 200 cysts/gram) but with *B. tepikiense* and round, brown *Protoperidinium* species and some *O. centrocarpun*. The Holocene contains much higher numbers of cysts (often > 3000 cysts per gram) with high numbers of *N. labyrinthus* and *O. centrocarpun*, together with an influx of *Impagidinium* spp., *Protoperidinium conicum*, *P. pentagonun* and *Spiniferites* spp. including *S. elongatus* and *S. unrabilis*.

SYNTHESIS

The dinoflagellate cyst record across the glacial/postglacial transition is similar in all four cores studied and a tentative synthesis can be made. It is convenient to attempt this in a series of time slices mimicking those used for the deglaciation history (Ruddiman 1987). Fortunately there is sufficient consistency between the studied sites to make this approach realistic; marked differences thought to be of oceanographic significance are noted. The dinoflagellate cyst assemblages, their interpretations and the climatic and oceanographic implications are given below.

Late Glacial > 13000 YBP

Off the western coast of Scotland on the continental slope, the dinoflagellate cyst record from BGS Gravity Core 56/-10/47 for this time slice consists of a low diversity, poor recovery assemblage (see Table 4). Species present mostly include *B. tepikieuse*, round, brown *Protoperidiuium* cysts, together with minor amounts of *O. centrocarpun*. Certainly *B. tepikieuse* contributed most to this assemblage. In BGS Vibrocore 56/-10/84 (time slice not illustrated here) the situation is similar to that noted above (Harland, *unpublished data*) with, in addition, occasional specimens of *?Algidasphaeridium unintum* (Harland and Reid) Matsuoka and Bujak. Similar assemblages have also been described by Peacock *et al.* (1992) for Late Glacial sediments recovered in vibrocores, dated at > 15245 YBP, on the shelf area west of Scotland and also in similarly dated sediments, > 12785 YBP, from a nearshore situation in the North Minch (Graham *et al.* 1990).

Further out into the north-eastern Atlantic Ocean, in the proximity of the Rockall Plateau, sediments of this age proved barren of dinoflagellate cysts from DSDP Hole 552A but DSDP Hole 610A yielded similar assemblages to those described above. Assemblages for the latter site are,

HARLAND: NORTH ATLANTIC DINOFLAGELLATES

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therefore, like those on the continental slope and shelf. Furthermore, the dinoflagellate cyst assemblage described from Unit 1 of Stoker *et al.* (1989) from a vibrocore in the Faeroe-Shetland Channel is also comparable but contains rather more round, brown *Protoperidinium* cysts. However, it is difficult, if not impossible, to assign all these assemblages unequivocally to exactly the same time interval and so, therefore, they may provide information only on particular environments within the Late Glacial.

However, undoubtedly within this time the marine sediments provided a characteristic low diversity and low recovery flora, predominantly containing *B. tepikieuse* and round, brown *Protoperidinimu* cysts. This type of cyst assemblage is known to characterize cold, arctic-like environments with a minimum of North Atlantic Current influence (see Wall *et al.* 1977; Harland 1983; Mudie and Short 1985). The presence of round, brown *Protoperidinimu* cysts may indicate the possibility of sea-ice (Dale 1985) and high numbers of *B. tepikiense* possible meltwater influxes lowering the sea-water salinity. These interpretations are based on increasing knowledge of the ecology of modern dinoflagellate cysts. Additionally these sediments often contain high proportions of reworked palynomorphs indicative of the high levels of erosion from shelf areas (see Stoker *et al.* 1989).

Throughout this time, the area under consideration was entirely glacial, with little NAC influence and probably often near sea-ice. This compares well with the scenario illustrated by Ruddiman (1987).

Allerod/Bölling Interstade 13000-11000 YBP

This time slice includes the beginning of deglaciation in the North Atlantic Ocean. In the two BGS cores off the west coast of Scotland, this is indicated by both a sharp rise in diversity and in cyst recovery. In 56/-10/47 the rise in cyst recovery is somewhat stepped before reaching a peak of over 2000 cysts per gram of sediment. Text-figure 4 shows the clear predominance and importance of B. tepikiense and, to a lesser extent, the later influx of O. centrocarpun. The additional presence of Impagidiuium spp., N. labyrinthus, Protoperidinium conicum and P. pentagonum is also of importance. This situation is almost exactly mirrored in 56/-10/84 but without the O. centrocarpmu peak and the presence of the two *Protoperidininmi* species. Although not recognized in shelf sediments, the Allerød/Bölling Interstade was also noted in the nearshore sediments of the North Minch (Graham et al. 1990); here the same interval is represented by units D2 and D3, the former dominated by *Protoperidinium* cysts with considerable amounts of *B. tepikiense*, and the latter by high proportions of O. centrocarpum. Also consistently present are Spiniferites cysts such as S. lazus Reid and S. ramosus (Ehrenberg) Loeblich and Loeblich. This shows a remarkable compatability with the offshore record but contains more elements consistent with a nearshore shelf situation. Units D2 and D3 are conveniently constrained by ¹⁴C dates and are confidently assignable to the Windermere Interstade.

In the vicinity of the Rockall Plateau this time slice is characterized by a single sample in DSDP Hole 552A, and a rather better record in DSDP Hole 610A consisting of an increase in cyst diversity and recovery to a peak of 715 cysts per gram of sediment. The assemblage is dominated by *B. tepikiense* but also contains round, brown *Protoperidinium* cysts, *P. pentagonum* and some *Spiniferites* cysts together with *N. labyrinthus* towards the top. The basic dinoflagellate cyst signature, however, appears to be similar to that on the continental slope and in the nearshore area. Further north in the Northern Rockall Trough and the Faeroe–Shetland Channel, the dinoflagellate cyst assemblages of Unit 2 (Stoker *et al.* 1989) are somewhat different. Here the cyst flora remains dominated by *Protoperidinium* species, particularly round, brown cysts, with significant *O. centrocarpum* and other minor cysts. Although some amelioration is evident, rather cold and severe conditions nevertheless prevailed, possibly with the proximity of sea-ice. This may indicate the extent of retreat of the polar front during this time to a position on the Wyville-Thomson Ridge.

The Allerod/Bölling time slice, like that of the Late Glacial, yields a reasonably homogenous dinoflagellate cyst assemblage. This assemblage is dominated by *B. tepikiense* which may be

interpreted as indicating the release of large quantities of freshwater into the marine environment as the ice retreated. This caused a general lowering of the salinity of the surface water in the northeastern Atlantic Ocean. Since this phenomenon is recorded in the deep ocean, on the continental slope and on the shelf, it must have been a widespread and significant oceanographic event. Further north, in the vicinity of the Wyville-Thomson Ridge, the dinoflagellate cyst assemblages are indicative of more severe climatic conditions with similarities to the earlier Late Glacial, but showing some influence from the North Atlantic. Towards the later stages of the Allerod/Bölling, increased NAC influence is evidenced by the increased amounts of O. centrocarpmn and N. labyrinthus. The implication is that the polar front, or at least sea-ice, remained in the northeastern Atlantic until towards the end of the interstade. It is doubtful if any of the records discussed herein are complete, so some caution must be exercised in the interpretation of these results. Nonetheless it does seem clear that sea-ice remained in the area for much of the time, contributing to the freshwater input into the system and influencing the cyst assemblages. This may not accord in detail with Ruddiman (1987), but it may explain part of the feedback mechanism that released large quantities of freshwater, adding to that entering from the Laurentide ice sheet (Broecker et al. 1988, 1989), and returning the Atlantic to a more glacial scenario. The evidence of Baumann and Matthiessen (1992), from the Norwegian Sea at this time, also suggests that any influx of North Atlantic water would have been diluted by large volumes of meltwater.

Yomger Dryas 11000-10000 YBP

The Younger Dryas comprises an enigmatic return to cold climates following the initiation of the deglacial cycle and is the subject of much controversy.

The two continental slope cores off western Scotland revealed a marked and sudden decline in both cyst diversity and recovery. The assemblages return to those dominated by round, brown *Protoperidinium* cysts and *B. tepikiense*, together with some *O. centrocarpum* and *N. labyrinthms*. BGS Vibrocore 56/–10/84 appears to prove a thicker sequence of Younger Dryas sediments but the overall assemblage characteristics are the same as that noted above with, perhaps, further detail of the temporal changes in the cyst flux to the sediment. Of interest is the initial peak of *B. tepikiense* and a final peak of *O. centrocarpum* but without collaborative evidence it would be unwise to speculate further. In the nearshore North Minch Borehole 78/4 (Graham *et al.* 1990) Unit D4 is interpreted as of Younger Dryas age as indicated by radiocarbon dating. The dinoflagellate cyst assemblages are dominated by round, brown *Protoperidinium* cysts but also contain *O. centrocarpum* and *Spiniferites* spp. such as *S. lazus* and *S. ramosus*.

Further offshore in the vicinity of the Rockall Plateau, DSDP Hole 552A is barren of dinoflagellate cysts and DSDP Hole 610A appears to have an attentuated sequence. However, the assemblages are low in diversity and recovery containing *O. centrocarpuni* and *N. labyrintlms*. To the north, Unit 3 of Stoker *et al.* (1989) in both the North Rockall Trough and the Faeroe–Shetland Channel are characterized by *B. tepikiense* with *O. centrocarpuni* and *Spiniferites* cysts.

The interpretation of the Younger Dryas dinoflagellate cyst record is difficult. Without the knowledge and confidence that a full and complete sequence is available, much of the interpretation must be speculative. The cyst assemblages from the continental slope and the nearshore area certainly suggest a return to glacial-like conditions but there are sufficient numbers of temperate cysts of North Atlantic affinity to indicate a difference between this cold interval and that of the Late Glacial at > 13000 YBP. Perhaps the Atlantic Ocean was functioning more like the present than during full glacial times as Jensen and Veum (1990) have suggested. Perhaps the Atlantic Ocean oceanography did not fully return to its previous state and that some vestige of a NAC remained, feeding some warmer water to the higher latitudes.

Holocene 10000 YBP - Present

A major change in the dinoflagellate cyst assemblages, even greater than that at the initiation of the Allerod/Bölling Interstade, heralds the Holocene. In previous publications this transition has been described in a number of different ways including 'event 3' of Harland (1984) and the change from *B. tepikiense*-dominated assemblages to those characterized by *O. centrocarpum* (Harland 1988). In both instances, the detail of the transition from the Late Glacial to the Post Glacial was not available. However, Turon (1980, 1981) had earlier documented in detail this change in the dinoflagellate cyst assemblages across the Pleistocene/Holocene boundary in cores from Rockall Channel.

In the present study, the two DSDP cores clearly show typical Holocene assemblages characterized by high diversity and high cyst recovery to, in some cases, over 2000 cysts per gram of sediment. The assemblages, as intimated above, are usually characterized by *O. centrocarpum* together with *N. labyrinthus* and often contain such *Spiniferites* cysts as *S. elongatus* and *S. mirabilis* together with *Protoperidinium conicum* and *P. pentagonum*; cyst species such as *B. tepikiense* and round, brown *Protoperidinium* cysts are rarer. DSDP Hole 610A contains a particularly good Holocene dinoflagellate cyst spectrum that portrays an initial sharp rise in *N. labyrinthus* before its decline and a subsequent rise in *O. centrocarpum*. In other words, there is a definite pattern within the Holocene of the numbers of cyst species being incorporated into the bottom sediments. This is also observed within the less conspicuous and less numerous members of the assemblage such that, for instance, the *Spiniferites* species rise in numbers toward the later stages of the *N. labyrinthus* peak.

Closer inshore, within the two BGS cores taken on the continental slope, the Holocene appears to be much more complete and furnishes a more detailed dinoflagellate cyst spectrum. This is especially true for 56/-10/47 (Text-figure 4) where cyst recovery reaches over 10000 cysts per gram of sediment. The Holocene spectrum can be divided into a number of phases largely based upon the relative abundances of *O. centrocarpum* and *N. labyrinthus*. These phases are listed below.

Phase 1

Cyst numbers began to increase sharply from the low recovery of the Younger Dryas and contain *O. centrocarpum* together with round, brown *Protoperidinium* cysts, in addition to increasing numbers of *S. elongatus*, *S. mirabilis*, *P. conicum*, *P. pentagonum* and *Impagidinium* cysts. This phase may be present within the record of DSDP Hole 552A but does not appear to be present in Hole 610A.

Phase 2

This is represented by a distinctive peak in the *N. labyrintlus* curve as the general cyst recovery improves. It may be present within 610A but is certainly absent in 552A; the recognition of these phases is difficult and often dependent upon sampling interval and sedimentation rate.

Phase 3

This coincides with the maximum cyst recovery in 56/-10/47 and peaks in the curves of *O. centrocarpum, S. elongatus, S. mirabilis,* round, brown *Protoperidinium* cysts and *P. conicum.* It may also be present in 610A but not in 552A.

Phase 4

This is recognized by the return of a peak in the *N. labyrinthus* curve and some decrease in recovery of other cyst species. However, this reduction in cyst numbers is relatively small and certainly not of the order of those seen in the older glacial sediments. This phase does not seem to be present in either of the two DSDP holes.

Phase 5

This final phase comprises a rise in the cyst recovery and also in the curves of *O. centrocarpum*, *S. elongatus*, round, brown *Protoperidinium* cysts, *P. conicum* and *P. pentagonum*. This is accompanied by a decline in *N. labyrinthus* and *S. mirabilis*. Like the phase described above, this also does not appear to be present in the two DSDP holes.

This description relies heavily upon 56/-10/47 as a standard for the area and assumes that it has sampled a complete sequence, or at least the most complete sequence of the Holocene known to date from the offshore area; for the moment it has not been possible to test this assumption.

In BGS core 57/-10/84 it is possible to recognize a number of the phases described above. In particular, it would appear that phases 4 and 5 are present but that some of the older phases are not. However, there are certain differences between the two that complicate the issue, including the loss of cyst recovery at a mid-point in the sequence, and the coincidence of an *O. centrocarpum* and a *B. tepikiense* peak in the lower part of the sequence.

All the Holocene dinoflagellate cyst assemblages outlined above are similar, with the exception of increased numbers of shelf species in the BGS cores, as might be expected from their location. Otherwise, it would appear that the climatic and oceanographically controlled assemblages occur throughout the area and offer the potential of detailed correlation. The sequences of the Northern Rockall Trough and the Faeroe–Shetland Channel (Stoker *et al.* 1989) encompassed within Unit 4 are typically characterized by rich cyst recovery and dominated by *O. centrocarpun*. It is, however, difficult to place the assemblages with respect to the phases reported herein, as the sequence is only some 0.45 m thick and the data were collected as percentages and not as absolute numbers.

In contrast, the sequence from the North Minch (Graham *et al.* 1990) proved over 16 m of Holocene that was divisible into three units and four subunits. It is, therefore, attractive to regard these as directly correlatable with the five phases described above. However, the North Minch Holocene assemblages, confirmed by radiocarbon dating, are dominated by *Spiniferites* species especially *S. lazus, S. mirabilis* and *S. ramosus*, with *O. centrocarpun* being a minor component only and *N. labyrintlus* being absent. Only the use of chronostratigraphical methods can establish the equivalence of these two schemes but undoubtedly the potential of using dinoflagellate cyst analysis for these high-resolution investigations is demonstrated herein.

COMPARISONS AND DISCUSSION

The pioneering work of Turon (1980, 1981) on the Rockall Channel revealed similar dinoflagellate cyst spectra to those described herein. In particular, they displayed the same prominence and sequential arrangement of peak occurrences of the species *B. tepikiense*, *N. labyrinthus* and *O. centrocarpun* (see especially the record for core 73136). Differences in Turon's spectra are mainly confined to the occurrence of high percentages of *Impagidinium* species, particularly *I. sphaericum* in the Holocene parts of the sequences. This difference may reflect the offshore nature of Turon's sites and the increased oceanic nature of the environment of deposition; *Impagidinium* spp. are well known indicators of the oceanic realm (Wall *et al.* 1977). In addition, Turon's cores contained increased percentages of *B. tepikiense* in the late Holocene sediments; a situation not recognized here but may be explained by the transportation of cysts in cold bottom water currents, as the present oceanographic configuration became firmly established. Turon (1978) proposed that the changes in the Holocene dinoflagellate cyst assemblages might reflect differences in primary productivity. Such differences were linked to the availability of nutrients caused by alterations in storm tracks across the North Atlantic Ocean affecting the oceanography.

More recently, De Vernal *et al.* (1992) reviewed the dinoflagellate cyst record for Quaternary sediments from the North Atlantic and, in their discussion of short-term high-resolution data, included those of Turon (1980, 1981) and that of BGS Gravity Core 56/-10/47 discussed in detail herein. These authors pointed out that changes in the dinoflagellate cyst assemblages could effect direct and accurate ecostratigraphical correlations across the region that reflected synchronous, or

almost synchronous, changes in the environment. These changes were oceanographic in nature and occurred as a result of climate-forcing. In particular, marked oceanographic alterations are known to have occurred as the polar front moved across the area during deglaciation.

Mattiessen (1991), in work published on the dinoflagellate cysts of the Norwegian Sea, suggested that the North Atlantic has influenced the area since about 15 Ka. Modern circulation patterns were initiated around 10 Ka, with *N. labyrinthus* dominating the cyst assemblages, until between 6 and 7 Ka when the present oceanography was fully established. Further work by Baumann and Mattiessen (1992), utilizing both dinoflagellate cysts and coccoliths, established several distinct steps in Holocene oceanography, not unlike those discussed earlier for the north-eastern Atlantic. In particular, after the first initiation of the surface water circulation, slightly cooler water conditions are thought to have prevailed followed by a major change at the time of the climatic optimum (*c.* 6000 YBP) as the present hydrography became established; they also suggested that there is some evidence for a decrease in sea-surface temperatures since about 4000 YBP.

All previous work, and that described here, are similar in respect to the deglaciation history of the north-eastern Atlantic from the evidence furnished by dinoflagellate cyst assemblages. The initial phase, marked by Termination IA in the oxygen isotope signature, is uniquely characterized by the occurrence of high percentages of *B. tepikiense*, a cyst species known to favour north temperate to arctic environments and less than fully marine salinities. Although the NAC was probably active at this stage, it is thought likely that large quantities of meltwater were entering the system and effectively lowering the sea-surface salinity. This phenomenon itself might well have been sufficient to reduce the flow of NADW and hence trigger the return of conditions akin to the full glacial situation. The cyst assemblages recovered from Younger Dryas sediments, although low in numbers and diversity, do contain species associated with the activity of the NAC; they are not the same as those recovered from sediments associated with full glacial environments.

The dinoflagellate cyst assemblages obtained from the Holocene sediments have proved not to be uniform, but to show distinct changes in character. These changes echo those already documented by Turon (1980, 1981), De Vernal *et al.* (1992) and Baumann and Mattiessen (1992). Even after deglaciation had been achieved, major changes were occurring in the oceanography of the North Atlantic Ocean and Norwegian Sea. Despite proposals published by Turon (1978) and Baumann and Mattiessen (1992) as to the likely changes and their causes, it is unfortunately true that there are insufficient ecological data available to interpret the assemblages with any degree of confidence. However, palynologists working with pollen diagrams have long been able to subdivide their Holocene spectra based upon changes in climate. It is likely that both the fluctuations in pollen diagrams and in the dinoflagellate cyst assemblages are related, and may have the potential to assist in the elucidation of Holocene oceanographic and climate change. Perhaps notions of fluctuations in the position of the atmospheric jet-stream, the pathways of anticyclones and the alternation of dry and wet climates, first recognized in Scandinavia (Sernander 1908), together with changes in the oceanography of the North Atlantic and Norwegian Sea are all inextricably linked.

This paper has demonstrated that the study of dinoflagellate cyst assemblages through the last deglaciation gives an insight into changes that are occurring in the surface waters of the ocean at a time when the globe is moving from a glacial climate to that of the present day. However, there is a distinct need for additional ecological information on both dinoflagellates cysts and the individual species, to aid the interpretation of the recovered assemblages. In this respect the work of Dale and Dale (1992) is worth consideration, as it is the only available study that attempts to examine the nature of the dinoflagellate cyst flux to the bottom sediments.

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DSDP Hole	- 552A	DSDP Hole (510.4
CSB No.	Depth (m)	CSB No.	Depth (m)
9139	0.10	10 116	0.12
9140	0.18	10 117	0.30
9141	0.30	10 118	0.40
9142	0.39	10 119	0.60
9143	0.51	10 120	0.75
9144	0.62	10 121	0.90
9145	0.71	10 122	1.06
9146	0.78	10 123	1.20
9147	0.89	10 124	1.35
9148	1.00	10 125	1.48
BGS Vibro	core 57/-10/84	BGS Gravity	Core 56/-10/47
CSB No.	Depth (m)	CSB No.	Depth (m)
9099	Sea-bed	9588	Sea-bed
9100	0.10	9589	0.10
9101	0.20	9590	0.20
9102	0.30	9591	0.30
9103	0.40	9592	0.40
9104	0.50	9593	0.50
9105	0.60	9594	0.60
9106	0.20	9595	0.70
9107	0.80	9596	0.80
9108	0.90	9597	0.90
9109	1.00	9598	1.00
9110	1.10	9599	1.10
9111	1.20	9600	1.20
9112	1.30	9601	1.30
9113	1.40	9602	1.40
9114	1.50	9603	1.50
9115	1.60	9604	1.60
9116	1.70	9605	1.70
9117	1.80	9606	1.80
9118	1.90	9607	1.90
9119	2.00	9608	2.00

APPENDIX 1 List of samples

APPENDIX 2

Taxonomic listing of the dinoflagellate cysts

The dinoflagellate cyst taxonomy for Quaternary dinoflagellate cysts consists of a mix of that derived from palaeontology and phycology (see Harland 1982, 1983 for discussion). The list of taxa recovered in this study reflects that mix but allows for the best circumscription of the tax pending the release of a new classification of living and fossil dinoflagellates.

Division PYRRHOPHYTA Pascher, 1914 Class DINOPHYCEAE Fritsch, 1929 Order PERIDINIALES Haeckel, 1894 Family GONYAULACACEAE Lindemann, 1928

Bitectatodinium tepikiense Wilson, 1973 (see Harland 1983, pl. 43, figs 3–4). *Impagidinium aculeatum* (Wall) Lentin and Williams, 1981 (see Harland 1983, pl. 46, figs 1–3). I. paradoxum (Wall) Stover and Evitt, 1978 (see Harland 1983, pl. 46, figs 4-5).

I. patuluan (Wall) Stover and Evitt, 1978 (see Harland 1983, pl. 46, figs 6-7).

I. sphaericum (Wall) Lentin and Williams, 1981 (see Harland 1983, pl. 46, figs 8-9).

Lingulodinium machaerophorum (Deflandre and Cookson) Wall, 1967 (see Harland 1983, pl. 43, figs 5-6).

Nematosphaeropsis labyrinthus (Ostenfeld) Reid, 1974 (see Harland 1983, pl. 43, figs 7-8).

Operculodinium centrocarpum (Deflandre and Cookson) Wall, 1967 (see Harland 1983, pl. 43, figs 9-10).

Spiniferites elongatus Reid, 1974 (see Harland 1983, pl. 44, figs 7-8).

S. lazus Reid, 1974 (see Harland 1983, pl. 44, figs 11-12).

S. membranaceus (Rossignol) Sargcant, 1970 (scc Harland 1983, pl. 45, figs 3-4).

S. mirabilis (Rossignol) Sarjeant, 1970 (scc Harland 1983, pl. 45, figs 1-2).

S. ramosus (Ehrenberg) Loeblich and Loeblich, 1966 (see Harland 1983, pl. 45, figs 5-6).

Family PERIDINIACEAE Ehrenberg, 1832

Algidasphaeridium? minutum (Harland and Reid) Matsuoka and Bujak, 1988 (see Harland 1992*a*, pl. 5.2, fig. 14).

Protoperidiniuan conicoides (Paulsen) Balech, 1974 (see Harland 1983, pl. 47, figs 2-3).

P. conicum (Gran) Balech, 1974 (see Harland 1983, pl. 47, figs 9-10).

P. leonis (Pavillard) Balech, 1974 (see Harland 1983, pl. 47, figs 7-8).

P. pentagonum (Gran) Balech, 1974 (see Harland 1983, pl. 48, figs 2-3).

P. subinerme (Paulsen) Loeblich III, 1969 (see Harland 1983, pl. 47, figs 11-12).

Order GYMNODINIALES Lemmermann, 1910 Family POLYKRIKACEAE Kofoid and Swezy, 1921

Polykrikos schwartzii Bütschli, 1873 (see Harland 1983, pl. 48, figs 10-12).